



## Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at <http://about.jstor.org/participate-jstor/individuals/early-journal-content>.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

# THE AMERICAN NATURALIST

---

VOL. XLVIII

April, 1914

No. 568

---

## THE ORIGIN OF $\times$ CAPSELLA BURSA-PASTORIS ARACHNOIDEA

DR. HENRI HUS

UNIVERSITY OF MICHIGAN

SINCE Jordan<sup>1</sup> described a number of elementary species of *Capsella Bursa-pastoris*, their constancy has been a subject of cultural experiment. Herbarium material demonstrates the existence of numerous apparently undescribed forms. The finding of strikingly distinct forms, such as *Capsella Heegeri*<sup>2</sup> and, more recently, *C. Viguieri*,<sup>3</sup> the work of Almquist<sup>4</sup> and that of Shull have added to the interest which this species holds for the investigator. It was Shull who determined the zygotic constitution of various forms. To be able to demonstrate this with exactitude is of the greatest value since Bateson and Lotsy expressed their doubt as to the homozygosity of de Vries's *Oenothera Lamarckiana*. It was left to Nilsson<sup>5</sup> to clearly show its necessarily heterozygous character. The interest aroused by this paper<sup>6</sup> leads me to believe that an

<sup>1</sup> Jordan, A., "Diagnoses d'espèces nouvelles ou méconnues pour servir de matériaux à une flore réformée de la France et des contrées voisines." Paris, 1864.

<sup>2</sup> Solms-Laubach, H. Graf zu, "Cruciferen studien. I. *Capsella heegeri*, eine neuentstandene Form der deutschen Flora," *Bot. Zeit.*, 55: 167, pl. 7, 1900.

<sup>3</sup> Blaringhem, L., "Les transformations brusques des êtres vivants." Paris, 1911.

<sup>4</sup> Almquist, E., "Studien über die *Capsella Bursa-pastoris* (L.)," *Acta Horti Bergiani*, 4: No. 6, 1907.

<sup>5</sup> Heribert-Nilsson, N., "Die Variabilität der *Oenothera Lamarckiana* und das Problem der Mutation," *Zeitschr. f. ind. Abst. u. Vererb.*, 8: 89, 1912.

<sup>6</sup> Lotsy, J. P., "Fortschritte unserer Anschauungen über Deszendenz seit Darwin und der jetzige Standpunkt der Frage," *Progressus Rei Botanicae*, 4: 361, 1913.

account of certain cultures of *Capsella*, in which mutations were simulated, would be of timely interest.

During the winter of 1908-1909, I collected in a greenhouse at Ann Arbor, Michigan, and at the disposal of the Botanical Department of the University of Michigan, twelve rosetts of *Capsella Bursa-pastoris*, the leaves of which showed certain more or less striking morphological differences. With the hope of isolating certain biotypes, the rosetts were placed in pots and permitted to flower. No measures were taken to prevent the accidental transference of pollen, but the pots were placed about six inches apart. This, as will be shown later, is the only precaution necessary to guard against cross-pollination, provided the cultures are carried on in a greenhouse and during the winter months. After a portion of the seed had ripened, the plants, the majority of which retained their climax leaves, became herbarium specimens. More recently, after constant association has enabled me to detect minute differences, it has been possible to identify some of these plants with two of the biotypes described by Shull,<sup>7</sup> to wit, *rhomboidea* and *simplex*. At the time of collection, the differences were sensed, but could not be described technically, since the extent of the influence wielded by fluctuating variability was an unknown quantity. Never before had I so fully realized the truth of de Vries's statement.<sup>8</sup>

We are trained to the appreciation of the differentiating marks of systematic species. . . . Our minds are turned from the delicately shaded features which differentiate elementary species.

The seed obtained was sown in sterilized soil during the spring of 1910. From each seedpan 60 individuals were transplanted to flats. As the plants grew older, it was found that, with a single exception, the seedlings in each of the flats were uniform, but that the seedlings in the different flats were not alike, three types being distinguishable. The interest in these types, for the isola-

<sup>7</sup> Shull, G. H., "*Bursa bursa-pastoris* and *Bursa Heegeri*: Biotypes and Hybrids," Publ. No. 112, Carnegie Institution of Washington, 1909.

<sup>8</sup> de Vries, Hugo, "Species and Varieties," 689, 1905.

tion of which these cultures had been undertaken, soon was overshadowed by the behavior of the seedlings bearing the number 4,108.6 and which were the offspring yielded by a plant of a type not described by Shull and which I have named  $\times$  *Capsella Bursa-pastoris Setchelliana*, in honor of Professor William Albert Setchell.

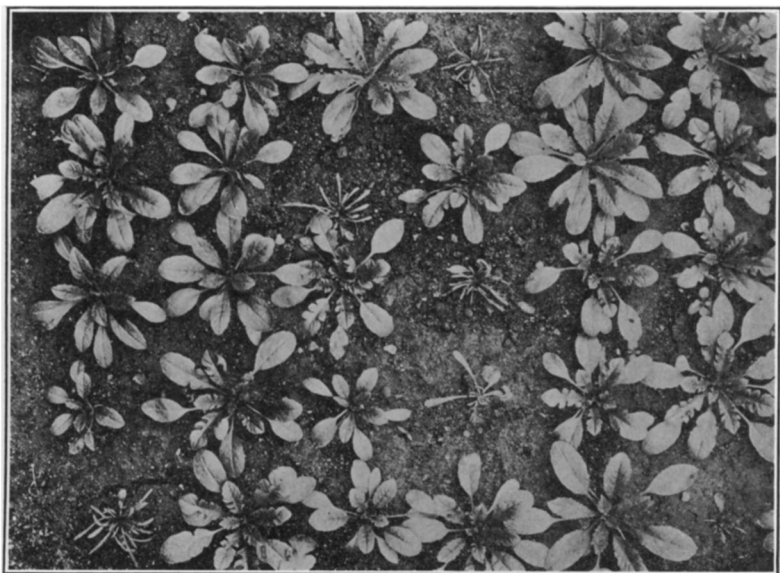


FIG. 1. APPEARANCE OF A LINEAR-LEAVED FORM AMONG SEEDLINGS OF *Capsella Bursa-pastoris*.

During the time that the seedlings remained in the seedpan, no deviations from the expected course of development were noted. However, after the seedlings had been transplanted to flats and had remained there a week or so, it became evident that some of the seedlings were not making the expected growth. Their development appeared most insignificant compared with that of the majority. A closer examination showed the cotyledons to be somewhat larger than normal and the leaves proper to be exceedingly small and almost linear. Nor did they attain the same length as the leaves of the rosetts belonging to other types.

An explanation of this peculiar development was sought in a possible attack on the part of either fungi or bacteria or in soil conditions. But the latter were uniform for the entire flat. Neither fungi nor bacteria could be demonstrated nor did the underground portion of the "abnormal" plants look unhealthy or underdeveloped.



FIG. 2. SEEDLINGS OF *x C. . . . Setchelli* AND *x C. . . . arachnoidea*

At this stage the flat presented the appearance shown in Fig. 1. At the time but three types were distinguished, the first of these constituted by plants which showed an incision of the blade, the second composed of those which apparently had entire leaves, and a third, comprising the small and linear-leaved rosetts, which, because of the spider-like appearance of the latter, has been designated *xCapsella Bursa-pastoris arachnoidea*. There also appeared a

single individual which, while closely resembling the form *arachnoidea*, differed from it in having somewhat spatulate leaves. This plant, a plant of *arachnoidea* and two of *Setchelliana*, are shown in Fig. 2.

After photographs had been taken, the plants were potted and placed in the frames. None of the plants made a growth as vigorous as that of the *Capsellas* growing in the open. The plants of the form *arachnoidea* developed leaves with a greatest length of 15 mm. and a greatest width of a little over 1 mm., causing the plant to retain its spider-like appearance. The roset with spatulate leaves appeared somewhat more vigorous, the average leaf measuring 22 mm. in length, with a greatest width of 2.5 mm. In later generations I have been able to obtain rosetts of *arachnoidea* with a greatest leaf-length of 100 mm. and a greatest width of 6 mm.

In the frames, flowering shoots made their appearance, those on *arachnoidea* being remarkable chiefly because of their small size, reaching a length not exceeding 12 cm. The flowers were small but well-formed. No well-developed pollen could be demonstrated. Seed did not form and the capsules retained their original form, typical of non-fertile capsules in *Capsella Bursa-pastoris*, reminding one of the capsules of *Capsella Heegeri*. They do not resemble the fertile capsules of *C. procumbens*. In the next generation I saw a single capsule formed on *arachnoidea* as the result of cross-fertilization, and in this case it differed in no manner from the normal capsule such as we know it in *Capsella Bursa-pastoris*.

The "normal" plants, *i. e.*, all those not belonging to the form *arachnoidea*, matured a large amount of seed. No measures were taken to prevent cross-pollination, but no other plant of *Capsella Bursa-pastoris*, within a radius of twenty feet, was in flower.

At this time, another attempt was made to group the plants. It was found that the criterion used earlier, *i. e.*, the incision of the blade, no longer could be relied upon, since plants, which at the time of the previous count, had shown an entire margin, now were more or less incised.

Unfortunately, after the seed had been collected, the plants were destroyed, having lost their climax leaves. An attempt to group them later with the aid of photographs failed, because photographs of all plants were taken during the earlier stages only, *i. e.*, before the appearance of the climax leaves. Another classification, for which climax leaves are not essential, and which is based upon the relative width of the first six or eight leaves, yields for 54 plants the proportion: "wide" 31, "narrow" 16, "linear" 7, the ideal proportion, as since worked out, being 33:16:16. The fact that the number for "linear," which represents the form *arachnoidea*, is too small by 9, may be ascribed to various circumstances, among others the fact that the last row in the flat did not appear in the photograph upon which the count was based. It is in the last row of a flat one ordinarily meets with the smaller or at least less vigorous individuals and it is very probable that in this last row occurred a large percentage of individuals belonging to *arachnoidea*. Furthermore, not all the seedlings, but only sixty, were taken in each case. Almost unconsciously one selects the largest individuals when transplanting from seedpan to flat. It is probable that in this process there were eliminated a greater percentage of seedlings of the linear form than of any of the others. Hence no great weight can be attached to the proportion obtained.

The collection of seed brought the work for 1910 to a close. As far as I was aware, no forms similar to *arachnoidea* had been either noted or described by any one who had devoted his time to culture experiments with *Capsella*. Neither Shull in America, nor Almquist in Sweden, nor Lotsy<sup>9</sup> in Holland, has made mention of such forms in their publications. The fact that no seed was produced by the aberrant form seemed to hold out little hope for the continuation of the cultures, and the sole trace left by this new form, if taxonomic form it was, threatened to consist of but a few photographs and some alcohol specimens. A single possibility presented itself.

<sup>9</sup> Lotsy, J. P., "Vorlesungen über Deszendenztheorien," 1: 180, Jena, 1906.

Whether the parent plant was of a hybrid character or whether the parent plant was mutating, and the new form or forms were to be looked upon as mutants, in either case there existed the possibility, if not the probability, that from the seeds obtained from those plants of the second generation which appeared "normal," a third generation might be obtained which would again present the abnormal form. Such indeed proved to be the case.

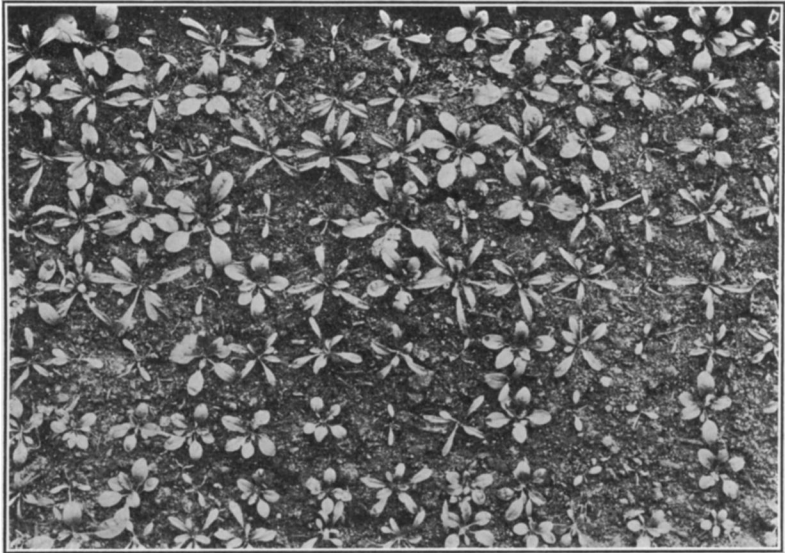


FIG. 3. EARLY STAGES IN THE DEVELOPMENT OF BROAD-LEAVED, NARROW-LEAVED AND LINEAR-LEAVED FORMS OF *Capsella*.

The seed for the next generation was obtained from 19 plants. The seed was sown separately in pots of sterilized soil. Certain of the parent plants, which we now identify with Shull's *simplex* and *rhomboidea*, produced a uniform, broad-leaved offspring. Others behaved like the parent, the form *arachnoidea* appearing in 197 individuals out of a total of 979, which does not include the 713 which bred true to the broad type. (For an illustration of these types see Fig. 3.)

It is unnecessary to go into details as to the various theories which suggested themselves as a solution of the



origin of the linear-leaved form which, because of its striking appearance, concentrated the attention upon itself. That perhaps we were dealing with a mutation was a thought which most naturally obtruded itself upon the mind of one who, for years, had fruitlessly tested a large number of species in the hope of discovering a case analogous to that of *Oenothera Lamarckiana*.<sup>10</sup> The possibility of a cross between a local form and either *Capsella Heegeri* or *C. procumbens*, suggested itself. However, the seedling stage of either of these two forms does not bear the remotest resemblance to that of *Capsella arachnoidea*. At the same time there was slight reason for believing that either *Capsella Heegeri* or *Capsella procumbens* ever had been grown in Ann Arbor.

During 1911 and the greater part of 1912, the problem rested here, no satisfactory explanation being found. But pedigree cultures were continued until, on the one hand, we succeeded in placing the plants in optimum surroundings for the production of climax leaves, and on the other began to distinguish between the various biotypes.

### THE BIOTYPES

As has been noted previously, it was possible to use two criteria for the classification of the rosetts. Leaving out of consideration the rosetts of the linear-leaved *arachnoidea*, it was found that after dividing the rosetts according to the "broad" or "narrow" character of the earlier leaves (Fig. 3), it was possible to further subdivide each group on the basis of the marginal indentation of the leaves subsequently formed.

I. *The "Broad" Group*.—Here the first four or five leaves possess a blade which is approximately twice as long as broad. Up to this stage the margin remains entire. When the sixth leaf appears one ordinarily can begin to distinguish between two types. These are:

*Type 1*.—In this, the first of the two broad-leaved forms, the margin of the first eight leaves remains entire,

<sup>10</sup> Hus, H., "The Origin of Species in Nature," AMERICAN NATURALIST, 45: 646, Nov., 1911.

showing at most a very slight crenation (Fig. 4). Usually the ninth leaf, though sometimes it is the eighth and sometimes the tenth, shows a more marked indentation, though seldom of a depth of more than 2 mm. on each side of the leaf and slightly below the middle. Subsequent leaves show an increase in the number and depth of the

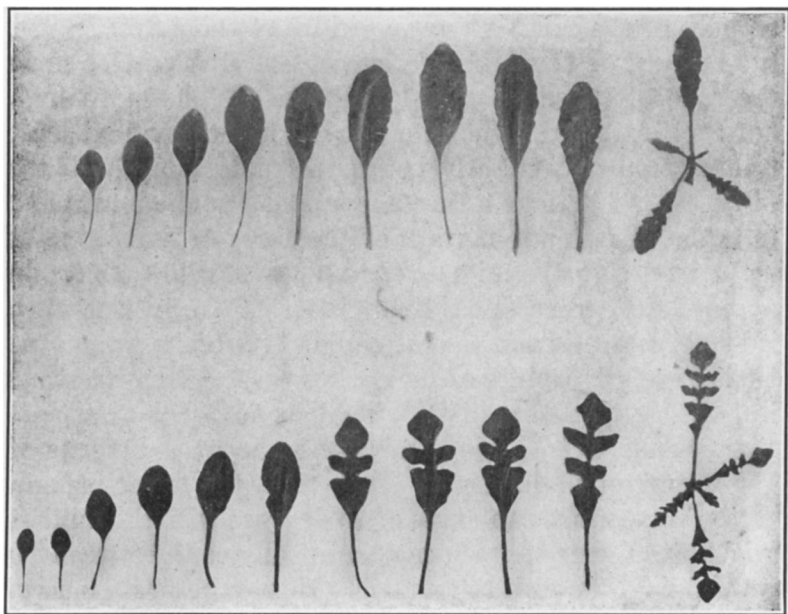


FIG. 4. DISSECTION OF YOUNG ROSETTS OF *C. . . . simplex* AND *C. . . . rhomboidea*, SHOWING THE "BROAD" CHARACTER OF THE EARLIER LEAVES AND THE DISTINCTIVE CHARACTER OF THE FIRST SINUS.

indentations, the maximum for both being reached in the climax leaves, which usually show five indentations reaching about midway from margin to midrib. In those of the earlier leaves which show a marked incision the lobes are obtuse. In the later leaves the lobes become acute. It may be stated as a general truth, that an increase in the depth of the sinus carries with it an increase in sharpness of the lobe. There is no secondary lobing, but sometimes the margin of the sinus shows a slight denticulation. While in the earlier leaves the sinuses separating the terminal lobe from the rest of the blade are the deepest,

the converse is true in the later leaves, where the sinuses separating the terminal lobe are the most shallow. I have identified this form with Shull's *simplex*.<sup>11</sup> My plants also agree fairly well with the illustration of ontogenetic succession of leaf forms in *Bursa* . . . *simplex*, shown by Shull.<sup>12</sup>

*Type 2.*—In the second of the two forms distinguished because of the greater relative width of their first leaves, the margin of the first five leaves remains entire, as in the case of those of type 1 (*simplex*). The sixth leaf, however, ordinarily shows a marked indentation, at least 3 mm. deep and slightly below the middle of the blade (Fig. 4). This indentation may appear in one margin or in both. The lower margin of the sinus ordinarily is at right angles to the midrib, the upper margin making an angle of 45 degrees with the midrib (Fig. 7, *b*). Even when it has become difficult to distinguish between types on the basis of relative width of the earlier roset leaves, it always is possible to distinguish between type 2 (*rhomboidea*) and type 4 (*Setchelliana* and *Treleaseana*), by means of the character of the sinus. In type 4, the lower margin of the sinus makes an angle of 45 degrees with the midrib, while the upper margin makes an angle of between 30 and 45 degrees with the midrib. Hence the first sinus in *C. . . . Setchelliana* and *C. . . . Treleaseana* is at least 90 degrees, while the first sinus in *rhomboidea* measures seldom more than 45 degrees and frequently less.

The seventh leaf of plants belonging to type 2 ordinarily shows two indentations on both sides of the leaf, dividing the blade into a lower portion, two central lobes and a terminal lobe. The depth of the incision amounts to about three-fourths of the width of the blade from midrib to margin.

It is possible to delay the appearance of the first indentations by transplanting from seedpan to flat either too early or too late. In such cases, the indentations appear in the seventh leaf only, or even later, and are rather

<sup>11</sup> *Loc. cit.*, 25, and Pl. 2, Fig. 2.

<sup>12</sup> Shull, G. H., "Verh. d. naturf. Ver. in Brünn," 49, Pl. 4, 1911.

shallow, reaching a depth of three-fourths of the width of the leaf from margin to midrib in the eighth, ninth or tenth leaf. However, once the indentations have made their appearance, the leaf next produced ordinarily shows two sinuses on both sides of the blade, usually the upper set, rarely the lower, being the deeper of the two, and almost reaching the midrib. The succeeding leaves show an increase in the number of lateral lobes from two to six. Since the incisions almost, if not quite, reach the midrib, both lateral lobes and the terminal lobes are well defined. Upon the lateral lobes secondary lobes appear, both on the distal and proximal margins. It is to be noted that only the climax leaves of well-grown specimens of the homozygotic form distinctly show the lobing of the proximal margin and this only on the middle lobes. The lobing of the primary lobes results in the setting off of a small terminal portion of each lateral lobe, which possesses a more or less rhomboidal form. This terminal lobe of the primary lobe can be observed to advantage only in the climax leaves of well-developed specimens.

I have no hesitation in identifying type 2 with Shull's *rhomboidea*.<sup>13</sup>

*Capsella Bursa-pastoris simplex* and *C. Bursa-pastoris rhomboidea*, described, respectively, as types 1 and 2, agree in having the first five or six leaves twice as long as broad, thus contrasting sharply with the plants to be described under types 3 and 4, which constitute the "narrow" group.

II. *The "Narrow" Group*.—In the plants belonging here, the first five or six leaves possess a blade which is from  $2\frac{1}{2}$  to 3 times as long as broad. Usually after the appearance of the seventh leaf, sometimes not until the appearance of the tenth leaf, it is possible, on the basis of marginal indentation, to separate the plants with "narrow" roset-leaves into two groups, designated respectively types 3 and 4.

*Type 3*.—Rosets of plants belonging to type 3 can not be distinguished from those of type 4, until after the

<sup>13</sup> Shull, Verh., Pl. 2; Biotypes, Pl. 1, Fig. 2.

seventh leaf has appeared (Fig. 5). It is to be noted that for the first six leaves of type 4, the ratio between mean length and width is 6:2, while for the corresponding leaves of type 3, the same ratio is 5:2. Once the seventh

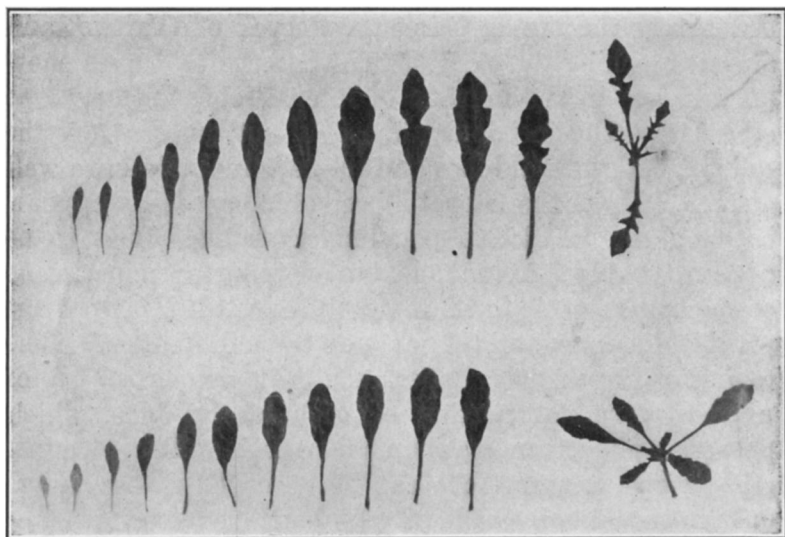


FIG. 5. DISSECTION OF YOUNG ROSETTS OF  $\times C. \dots$  *Setchelli* AND  $\times C. \dots$  *attenuata*, SHOWING THE "NARROW" CHARACTER OF THE EARLIER LEAVES AND THE DISTINCTIVE CHARACTER OF THE FIRST SINUS.

leaf has appeared, a distinction readily can be made, since in type 3, no sinuses appear, and the leaves, from the seventh to the tenth, might be mistaken for those of *simplex* (Fig. 5). Later leaves readily can be distinguished from those of *simplex*, by the pointed apex, the very shallow sinuses, ending in a sharp tooth, and by the fact that the greatest width of the blade lies above the middle, about one third the length from the tip (Fig. 6).

This form, which because of its morphological characters on the one hand, and its behavior in breeding on the other, can readily be distinguished from all others, I designate  $\times$  *Capsella Bursa-pastoris attenuata*.

*Type 4.*—Not only do the first leaves of plants, belonging to this type, differ in relative width from the first leaves of plants of *rhomboidea* and *simplex*, but there also

is a difference in the apex of the leaf, the apices of leaves of this type, like those of type 3, being decidedly pointed, while those of types 1 and 2 are rounded.<sup>14</sup>

At the sixth or seventh leaf stage, the marginal indentations make their appearance, at first as slight crenations, then as long and shallow sinuses, and finally, in the eighth or ninth leaf, as a sinus on one or both sides of the midrib and about the middle of the blade (Fig. 5). The lower margin of the first sinus ordinarily makes an angle of 45 degrees with the midrib, while the upper margin makes an angle of from 30 to 45 degrees with the midrib. This renders the first sinus ordinarily greater than 90 degrees (Fig. 7, *a*). The depth of the first sinus is approximately one half the distance from margin to

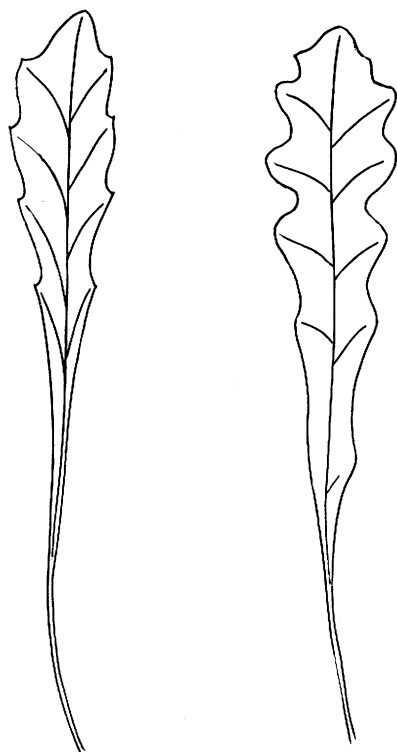


FIG. 6. LATER ROSET LEAVES OF  $\alpha$  *C.*  
... *attenuata* AND *C.* ... *simplex*.

midrib. In subsequent leaves the depth increases, so that in the 11th leaf the sinuses almost reach the midrib. In *Treleasi*, one of the two forms, which together constitute type 4, the climax leaves show incisions to the midrib, and a well-marked terminal lobe, while in the other the sinuses are less deep but the terminal lobe still is well marked (Fig. 8). The number of sinuses increases in propor-

<sup>14</sup> It is to be noted that in my cultures there appear, from time to time, plants of *rhomboidea* of which the leaves have sharply pointed lobes. What relation these plants bear to others classed with them under *rhomboidea*, I am at present unable to say.

tion to their depth. If the seventh leaf has one sinus in each margin, the eighth and ninth usually have two, the tenth and eleventh, three, and so on, until the mean of six is reached. As the lobes increase in number, they

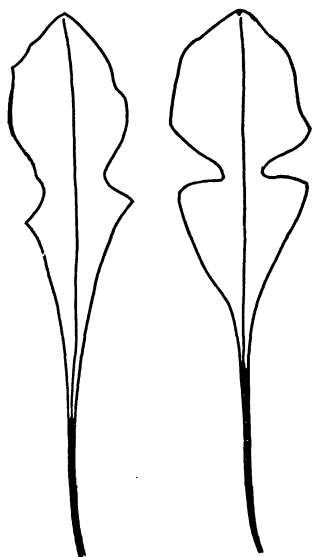


FIG. 7. EARLY ROSET LEAVES OF *x C. . . . Setchelli* AND *C. . . . rhomboidea*.

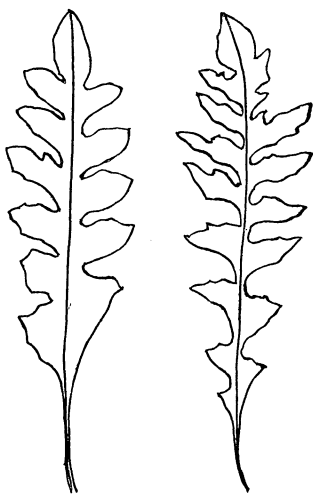


FIG. 8. CLIMAX LEAVES OF *x C. . . . Setchelli* AND *x C. . . . Treleaseana*.

not only become narrower but the sinuses do likewise. This is the result of a gradual increase in the angle between the lower margin of the sinus and the midrib. In the eighth leaf the lower margin forms an angle of about 90 degrees with the midrib, causing the formation of a primary lobe, triangular in shape and with an upper angle of about 45 degrees, instead of the 90-degree angle found in the first lobe. In older leaves the angle between lower margin of sinus and midrib may increase to 110 or even 120 degrees. The climax leaves therefore get to resemble more and more those of *rhomboidea*, especially since the distal margin of the sinus, from the tenth leaf on, exhibits a number of denticulations which, in older leaves, especially of one of the forms (*Treleaseana*), tend to become incisions, so that secondary lobes are

formed. However, the end of the lobes of early leaves of type 4 always are sharply pointed (Fig. 9), while the lobes of early leaves of *rhomboidea* are ordinarily rounded at the ends (Fig. 4).

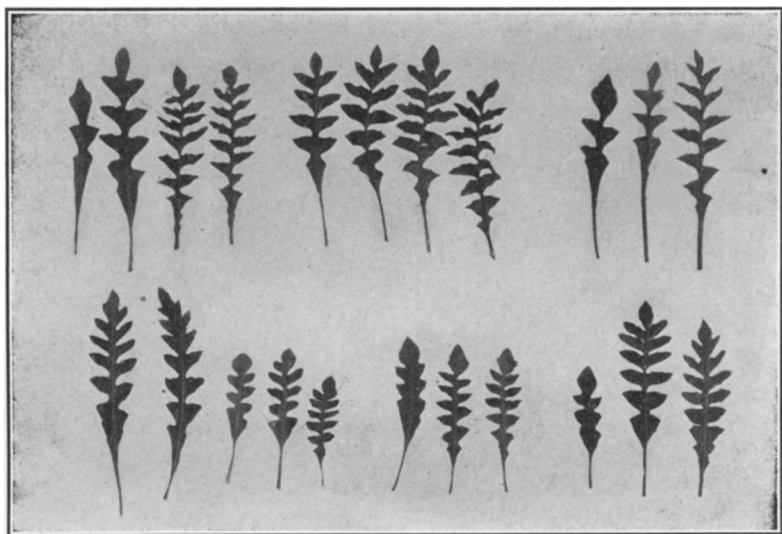


FIG. 9. UPPER ROW: 3 SETS OF LEAVES FROM AS MANY PLANTS OF  $\times$  *C. . . . Treleasei*. LOWER ROW: 4 SETS OF LEAVES FROM AS MANY PLANTS OF  $\times$  *C. . . . Setchelli*.

From a morphological point of view these leaves are entirely different from any form described by Shull, the differences being most marked and very readily recognized once our attention has been called to them. But it is especially the behavior of the plants on breeding which leads me to recognize them as most distinct hybrid forms and which I have designated  $\times$  *Capsella Bursa-pastoris Setchelliana* in honor of Professor William Albert Setchell, and  $\times$  *Capsella Bursa-pastoris Treleaseana*, in honor of Professor William Trelease.

*Type 5.*—*Capsella Bursa-pastoris arachnoidea*. This form, which readily is recognized from the first by its linear leaves, does not require an elaborate description at present, since it will be discussed in detail later. It has been illustrated in Figs. 1, 2 and 3.



The above descriptions apply only to plants grown under fairly uniform conditions, in a light soil in a greenhouse, and treated in such a manner as to offer the plant the most favorable conditions for development. By leaving the plants too long in the flats, so that crowding results, by keeping them too moist and warm, etc., it is possible to produce abnormal climax leaves in which the typical differences can be recognized with difficulty only. By leaving plants too long in the seedpans, by keeping them too dry, it may be brought about that plants flower without having produced climax leaves. There will be doubtless many who, because of this, will refuse recognition to the segregates just described. "Quæcunque dixi, si placuerint, dictavit auditor." Fortunately, the differences of behavior on breeding are such, we must recognize their distinct genotypic constitution.

#### GENOTYPIC CONSTITUTIONS

Shull, in the papers above quoted, made one of the most important of recent contributions to science, since he determined with exactitude the relations existing between some of the lesser forms which, because of their alleged constancy or inconstancy, have been a bone of contention since the days of Jacquin. Making extensive cultures of *Capsella*, Shull was able to distinguish four forms (Fig. 10), to wit, *heteris*, with leaves divided to the midrib, with

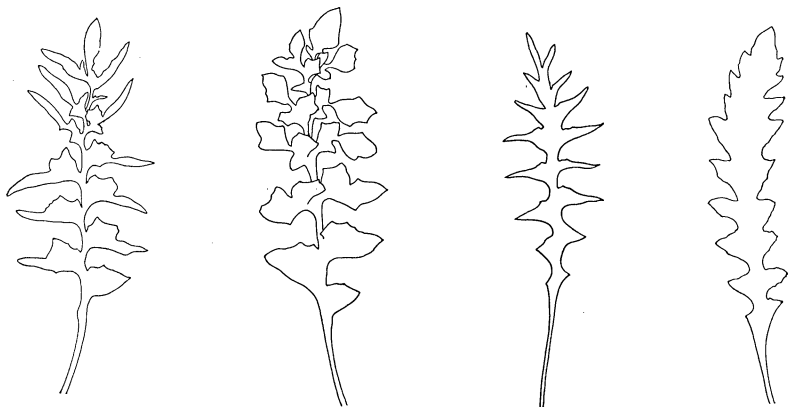


FIG. 10. CLIMAX LEAVES OF *C. . . . heteris*, *C. . . . tenuis*, *C. . . . rhomboidea* AND *C. . . . simplex*.

elongated primary lobes, a marked secondary lobe, in the distal axil of the primary lobe and a well-marked terminal lobe; *rhomboidea*, with leaves divided to the midrib, with an unelongated primary lobe, with an incision in the distal margin setting off a secondary lobe and a corresponding incision on the proximal margin of the primary lobe, setting off, in well-grown specimens, a terminal portion of each lateral lobe, generally of rhomboidal form; *tenuis*, with the elongated primary lobe of *heteris*, but with a sinus which usually does not reach the midrib, terminal lobe clear cut; *simplex*, with lateral lobes obtuse, never attenuated, the incisions being shallow and never reaching the midrib.

Shull recognized here the presence and absence of two factors, one (*A*) responsible for the sharp primary lobe of *heteris* and the attenuation of the lobes in *tenuis*, while the other (*B*) is responsible for the division of the leaf to the midrib, the definite terminal lobe and the secondary lobes. On this basis Shull was able to represent the biotypes by conventional Mendelian symbols, thus: *heteris*, *AB*; *rhomboidea*, *aB*; *tenuis*, *Ab*; *simplex*, *ab*.

That this conventional presentation gives us a reliable working basis, my experiments have shown most satisfactorily. With the aid of these symbols I have been able to solve the origin of *Capsella arachnoidea*, the experiments showing that, without question, forms presenting the spider-like appearance of the rosetts typical of this plant are of hybrid origin.

#### THE ZYGOTIC CONSTITUTION OF 4,108.6

The problem to be solved was that of the zygotic constitution of the original parent, the plant which in my notes is recorded as 4,108.6. Among its offspring neither *heteris* nor *tenuis* made their appearance, while both *rhomboidea* (*aB*) and *simplex* (*ab*) were met with. Hence the parent was homozygotic for (*a*), but heterozygotic for (*B*). Therefore, its zygotic constitution, in part, must have been *aaBb*.

Besides *rhomboidea* and *simplex* there appeared two

forms, referred to as types 3 and 4, the latter being capable of further subdivision. Neither of these was described by Shull. At least one difference between *rhomboidea* and *simplex*, on the one hand, and types 3 and 4, on the other, could be noted at once, *i. e.*, the relative width of the leaf. As has been shown above, the former have their first leaves twice as long as broad, the latter three times as long as broad. The idea suggested itself that there might exist a factor which determined these characters. Since the original parent belonged to type 4, the narrow character of the earlier leaves must be dominant over the broad character. Also, since the original parent produced both "narrow" and "broad" types, it must have been heterozygotic for this character. Using (*N*) to indicate the gene, we get for the zygotic construction of the parent plant *aaBbNn*.

	<i>aBN</i>	<i>aBn</i>	<i>abN</i>	<i>abn</i>
<i>aBN</i>	1 <i>aBN</i> <i>aBN</i>	2 <i>aBn</i> <i>aBN</i>	3 <i>abN</i> <i>aBN</i>	4 <i>abn</i> <i>aBN</i>
<i>aBn</i>	5 <i>aBN</i> <i>aBn</i>	6 <i>aBn</i> <i>aBn</i>	7 <i>abN</i> <i>aBn</i>	8 <i>abn</i> <i>aBn</i>
<i>abN</i>	9 <i>aBN</i> <i>abN</i>	10 <i>aBn</i> <i>abN</i>	11 <i>abN</i> <i>abN</i>	12 <i>abn</i> <i>abN</i>
<i>abn</i>	13 <i>aBN</i> <i>abn</i>	14 <i>aBn</i> <i>abn</i>	15 <i>abN</i> <i>abn</i>	16 <i>abn</i> <i>abn</i>

FIG. 11. DIAGRAM TO ILLUSTRATE THE NATURE OF THE OFFSPRING OF  $\sigma$  C. . . . *Setchelli* (*aaBbNn*).

Since self-fertilization is the rule in *Capsella*, it was an easy matter to test the validity of the theory. A form *aaBbNn*, one with unelongated primary lobes, sinuses reaching the midrib and with early leaves of a "narrow" type should yield, on self-fertilization, the following combinations: 1. *bbnn* (square 16), a plant of which, according to our definition, the earlier roset leaves should be

broad and of which the later leaves shall lack incisions reaching to the midrib, a plant, in short, which should have all the characteristics of Shull's *simplex*. Furthermore, on being selfed, it should yield a uniform offspring, in all respects resembling the parent.

Such plants actually were encountered. Of the plants grown to maturity, twelve were selected as seed-bearers. All bore the *simplex* character. Ten of these plants were selected from among the first generation of plants of the supposed zygotic constitution *BbNn*, while one parent (yielding No. 25,712) was derived from a plant bearing the *simplex* character and another (yielding No. 31,112) was derived from a plant which was shown to have the zygotic constitution *bbNn*.

TABLE I  
EVIDENCE OF HOMOZYGOTIC CHARACTER OF *Simplex* (*bbnn*)

Index Number	Number of Plants		Index Number of Parent	Character of	
				Parent	Grand-parent
25,712	78	<i>G</i> <sup>15</sup>	8,112 <i>BR</i> 12 <i>P</i> 9	<i>bbnn</i>	<i>bbnn</i>
25,912	22	<i>G</i>	8,212 <i>BR</i> 3 <i>P</i> 1	<i>bbnn</i>	<i>BbNn</i>
26,312	42	<i>G</i>	8,212 <i>CR</i> 5 <i>P</i> 1	<i>bbnn</i>	<i>BbNn</i>
26,512	187	<i>G</i>	8,212 <i>FR</i> 3 <i>P</i> 3	<i>bbnn</i>	<i>BbNn</i>
26,712	180	<i>G</i>	8,212 <i>HR</i> 7 <i>P</i> 7	<i>bbnn</i>	<i>BbNn</i>
30,012	276	<i>O</i>	8,212 <i>CR</i> 5 <i>P</i> 1	<i>bbnn</i>	<i>BbNn</i>
30,112	108	<i>O</i>	8,212 <i>HR</i> 2 <i>P</i> 6	<i>bbnn</i>	<i>BbNn</i>
30,212	60	<i>O</i>	8,212 <i>GR</i> 6 <i>P</i> 8	<i>bbnn</i>	<i>BbNn</i>
30,312	162	<i>G</i>	8,212 <i>GR</i> 6 <i>P</i> 8	<i>bbnn</i>	<i>BbNn</i>
30,712	27	<i>O</i>	8,212 <i>HR</i> 3 <i>P</i> 6	<i>bbnn</i>	<i>BbNn</i>
31,112	50	<i>O</i>	26,012 <i>AR</i> 7 <i>P</i> 6	<i>bbnn</i>	<i>bbNn</i>
3,113	207	<i>O</i>	26,912 <i>BR</i> 1 <i>P</i> 3	<i>bbnn</i>	<i>BbNn</i>
	1,399				

This table offers an excellent illustration of the small danger of an accidental cross, even if the plants are not guarded, always, of course, when the proper precautions, indicated above, are taken. Numbers 26,312 and 30,012, as well as numbers 30,212 and 30,312, respectively, offer instances of uniform inheritance in plants possessing recessive characters only and of which the parents in the one case were left unguarded, in the other caged. Had

<sup>15</sup> In this column "*G*" indicates that the parent plant was guarded, "*O*" that the plant was open-fertilized. In other tables the same abbreviation will be used.

crossing taken place in the case of the unguarded flowers, this would, because of the purely recessive characters possessed by *simplex*, have become apparent at once. In all cases the parents were checked by means of herbarium specimens or photographs, or both.

2. *bbNN* (square 11). According to our hypothesis, a plant of this zygotic construction should have the earlier roset leaves narrow and the climax leaves should lack incisions to the midrib. It also should breed true. A plant fulfilling these conditions has not been encountered, or rather, its recognition was delayed until the offspring of the corresponding heterozygote *bbNn* could be observed. As will be shown, the zygotic combination *bbNN* yields a plant with the external characteristics of *arachnoidea*.

3. *bbNn* (squares 12 and 15). A plant of this zygotic constitution should have narrow early leaves and the climax leaves should lack incisions to the midrib. On self-fertilization it should yield 25 per cent. *bbNN*, 50 per cent. *bbNn* and 25 per cent. *bbnn*.

<i>bN</i> <i>bN</i>	<i>bn</i> <i>bN</i>
<i>bN</i> <i>bn</i>	<i>bn</i> <i>bn</i>

Several plants were found which fulfilled the requirements as to leaf characters. Such plants, on being selfed, yielded approximately 25 per cent. *simplex*, which we know to have the zygotic constitution *bbnn*, while about 50 per cent. bore the parental characters, supposedly represented by *bbNn*. The remaining 25 per cent. clearly belonged to the type *arachnoidea*. In all, 12 plants were selected as seed-bearers, some being guarded, others remaining uncaged. The results are given in Table II.

The totals closely approximate the Mendelian ratio, yielding, respectively, *bbNN* 24 per cent., *bbNn* 49 per cent. and *bbnn* 27 per cent. Having established the identity of *bbnn* (*simplex*) and *bbNn* (*attenuata*), we are forced to recognize *bbNN* as the zygotic construction of *arachnoidea*. It would be a comparatively easy matter to test

this directly, provided the form *arachnoidea* produced seed. Though I have grown several hundreds of these plants, I have obtained in all but eight seeds, and these as the result of hybridization. Hence the test must be made indirectly through crossing of forms yielding the desired gametic combinations.

TABLE II  
EVIDENCE OF HETEROZYGOTIC CHARACTER OF *attenuata* (*bbNn*)

Index Num- ber	Number of Plants						Index Number of Parent	Char. of Parent	G or O	Char. of Grand- parent
	<i>bbNN</i>		<i>bbNn</i>		<i>bbnn</i>					
	Found	Ex- pected	Found	Ex- pected	Found	Ex- pected				
26,012	19	25.50	56	51.00	27	25.50	8,212BR5P1	<i>bbNn</i>	G	<i>BbNn</i>
26,412	8	7.50	14	15.00	8	7.50	8,212DR10P8	<i>bbNn</i>	G	<i>BbNn</i>
31,212	16	14.75	27	29.50	16	14.75	26,012AR2P1	<i>bbNn</i>	O	<i>bbNn</i>
31,312	22	15.00	19	30.00	19	15.00	26,012AR1P2	<i>bbNn</i>	O	<i>bbNn</i>
31,412	10	14.25	25	28.50	22	14.25	26,012AR1P3	<i>bbNn</i>	O	<i>bbNn</i>
31,512	24	25.50	47	51.00	31	25.50	26,012AR1P4	<i>bbNn</i>	O	<i>bbNn</i>
31,612	2	2.50	4	5.00	4	2.50	26,012AR6P6	<i>bbNn</i>	O	<i>bbNn</i>
31,812	26	28.25	54	56.50	33	28.25	26,012BR1P3	<i>bbNn</i>	O	<i>bbNn</i>
31,912	11	16.50	40	33.00	15	16.50	26,012BR1P6	<i>bbNn</i>	O	<i>bbNn</i>
3,213	61	64.25	130	128.50	66	64.25	26,912DR2P4	<i>bbNn</i>	O	<i>BbNn</i>
3,313	70	61.50	117	123.00	59	61.50	26,912ER6P6	<i>bbNn</i>	O	<i>BbNn</i>
3,513	27	35.50	71	71.00	34	35.50	26,912FR6P4	<i>bbNn</i>	O	<i>BbNn</i>
Total .	296	308.50	604	617.00	334	308.50				

Of the twelve parent plants concerned in the above experiment, five were selected from among the first generation of a plant having the supposed zygotic constitution *BbNn*, while seven were the direct offspring of No. 26,012, which had been shown to yield the three forms, *arachnoidea*, *attenuata* and *simplex*, as indicated in Table II.

The *simplex*, obtained by selfing a plant of *bbNn*, breeds true, as indicated in Table I, No. 31,112, a *simplex*, yielding a uniform *simplex* offspring, consisting of 50 individuals.

4. *BBnn* (square 6). A plant of this supposed zygotic constitution should resemble, in all respects, Shull's *rhomboidea*, the earliest roset leaves being broad, and the incisions of the climax leaves reaching the midrib. It should breed true. Five lots, involving four parents, were grown. Again it was shown, in the case of No. 26,812 and

No. 30,612, that the fact that plants are left unguarded does not affect results. The parents, in all cases, were selected from among the first generation of plants having the supposed zygotic constitution  $BbNn$ . The results are given in Table III.

TABLE III  
EVIDENCE OF HOMOZYGOTIC CHARACTER OF *rhomboidea* ( $BBnn$ )

Index Number	No. of Plants	Index Number of Parent	Char. of Parent	G or O
25,812	20	8,212BR1P6	$BBnn$	G
26,812	80	8,412BR3P2	$BBnn$	G
27,012	6	8,412ER10P6	$BBnn$	G
27,112	210	8,412ER13P12	$BBnn$	G
30,612	96	8,412BR3P2	$BBnn$	O

In all cases the offspring was uniformly of the *rhomboidea* character.

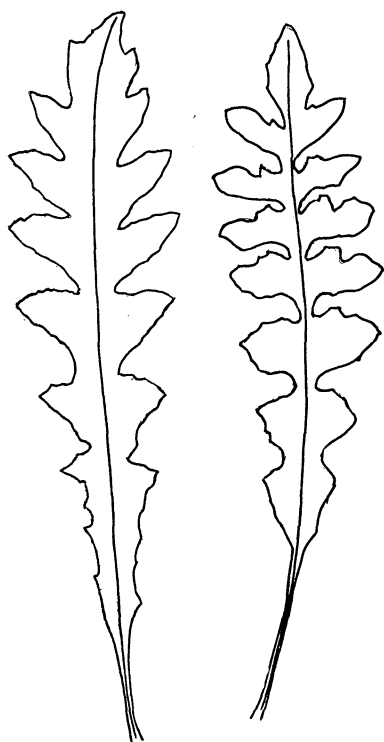


FIG. 12. CLIMAX LEAVES OF A HETEROZYGOTIC *C. . . . rhomboidea* AND OF A HOMOZYGOTIC *C. . . . rhomboidea*. . .

$Bn$	$Bn$
$Bn$	$bn$
$Bn$	$bn$
$bn$	$bn$

5.  $Bbnn$  (squares 8 and 14). Plants of this zygotic constitution should resemble those of the preceding group, but on being selfed should yield 25 per cent. homozygotic *rhomboidea* ( $BBnn$ ), 50 per cent. heterozygotic *rhomboidea* ( $Bbnn$ ) and 25 per cent. *simplex* ( $bbnn$ ).

These three forms were found to constitute the offspring of a single plant, 8,212HR1P3, itself an offspring of a plant of the supposed zygotic constitution  $BbNn$ . This plant, from

the first, was classified as a *rhomboidea*. At the present time, a photograph of the young roset confirms this classification. But two climax leaves, which, in the earlier part of these experiments, were deemed sufficient, show that the sinuses do not quite reach the midrib (Fig. 12). Unfortunately, Shull, in the description of his No. 054.28,<sup>16</sup> does not mention this point, though he does point out that "the later rosette-leaves had some of the secondary lobes acutish, but not elongated." In the older climax leaves, even of a homozygous *rhomboidea*, I find that the secondary lobes disappear. Shull, in the description just referred to, is so specific as to the typical *rhomboidea* character of the heterozygote that I have hesitated to classify the heterozygotes and the homozygotes. But the homozygotic *rhomboidea*, obtained as the extracted recessive of a selfed plant of the supposed zygotic constitution *BBNn*, always has sinuses which reach the midrib. In other combinations, also, one can distinguish between *BB* and *Bb* by the relative depth of the sinus. For the present, then, we will rely upon this character. In the case under discussion (26,612, the offspring of 8,212*HR1P3*, guarded) there were among the 39 plants 6 which clearly were *simplex*, the heterozygotic *rhomboidea* was represented by 22 individuals, and the homozygotic *rhomboidea* by 11 individuals, the calculated ratio being 9.75:19.50:9.75. The percentage of *simplex* is far too low, 15.4 per cent., instead of 25 per cent., but, considering the small number of individuals concerned, the total outcome is fairly satisfactory. It is almost unnecessary to add that in this, as in other cases, the offspring of the various plants is being tested as fast as time and facilities permit.

*Type 4.*—Having shown the presumable correctness of our supposition as to the zygotic constitution of the initial plant (*BbNn*), as far as the presence, appearance and behavior on breeding of *simplex*, *rhomboidea* and *attenuata* are concerned, there remains to identify the major group of combinations which, in a simple di-polyhybrid, constitutes



nine sixteenths of the total offspring and may be uniform in appearance, the constituents being separable only by breeding, "eine heillose Arbeit," as Baur has it. Fortunately, in this case, it is possible to distinguish readily between the various combinations.

One of the combinations, *BBNn* (square 1), should breed true, being homozygotic for both characters concerned. We would expect such a plant to have narrow first leaves and climax leaves with incisions to the midrib. Thus far I have not encountered such a plant, something which at one time led me to consider the possibility of gametic repulsion, in this instance the gamete *BN* being incapable of existence. This supposition seemed the more plausible since the two genes *B* and *N* well might be supposed to be antagonistic, the one being responsible for an incision of the leaf to the midrib, the other tending to make the leaf, especially the earlier leaves, narrow. Were this assumption correct, none of the zygotic combinations found in squares 1, 2 and 5, 3 and 9, and 4 and 13, would be formed, though we would expect the same combination as occurs in squares 4 and 13 to make its appearance as the result of the fusion of the gametes *bN* and *Bn* (squares 7 and 10).

Were this supposition correct, we should have a case similar to that of the sweet pea "Purple Invincible," and we could not expect the gamete (*bn*) to be formed. Since, however, *simplex* (*bbnn*) appears in our cultures, this theory must be rejected. Recently also, in culture No. 30,412, an instance was found in which the guarded parent, supposedly of type 4, yielded, not *simplex*, *rhomboidea*, *attenuata*, *arachnoidea* as well as the parental type, but only *arachnoidea*, *rhomboidea* and the parental type, and in proportions closely approximating a ratio 1:1:2.

A plant which yielded 25 per cent. *rhomboidea* and no *simplex*, must have been homozygotic for *B*, and since it yielded also 50 per cent. of type 4, must have been heterozygotic for *N*, its zygotic constitution therefore being *BBNn*. Such a plant, on self-fertilization, should yield 25 per cent. *rhomboidea*. Provided the homozygote and

the heterozygote have the same appearance, the remaining 75 per cent. should resemble the parent (Fig. 9, b).

$BN$ $BN$	$Bn$ $BN$
$BN$ $Bn$	$Bn$ $Bn$

But in one case (30,412), the parent being 8,412*BR9P9*, and open fertilized, the offspring consisted of 26.3 per cent. *rhomboidea*, 46.2 per cent. of the parental type and 27.5 per cent. *arachnoidea*. If our supposition as to the zygotic constitution of the parent is correct, then the zygotic constitution of the *arachnoidea* in this offspring must be *BBNN*. In the case of a selfed *attenuata*, we found that approximately 25 per cent. of the offspring was composed of *arachnoidea* of the probable zygotic constitution *bbNN*. Is it possible that any *Capsella*, homozygotic for *N*, would have the appearance of *arachnoidea*? This seems more than probable, and other evidence, to be adduced later, appears to support this view. The history of the *BBNn* is as follows:

During 1912 I grew No. 8,412 from seeds of a plant which resembled the grandparent 4,108.6. It was composed of 1,079 individuals, among which various types, such as "broad," "narrow" and "linear," could be recognized. Not all plants were thus classified, a fourth group of "intermediates" being formed, indicating that some of the plants, while in certain respects resembling *simplex* and especially *rhomboidea* (deep lobing, secondary lobes), in other characters more closely approximated the "narrows," since their early leaves had been noted as "narrow." In the light of recent experience, it is easy to see why the distinction was made, though at the time the conception of the differences was most hazy. Several of these "intermediates" were grown, and of these a single one yielded the seed for the next generation. This plant had been permitted to flower unguarded, but after a number of capsules had developed on the main stalk, this was decapitated and the sideshoots were allowed to de-

velop. At this time the entire plant was caged. Subsequently the seeds of the open fertilized and of the guarded flowers were sown separately, with the following results:

	30,412. Open Fertilized			30,512. Guarded		
	Per Cent.	Plants		Per Cent.	Plants	
		Found	Expected		Found	Expected
<i>Arachnoidea</i> . . .	27.5	40	36.25	21.15	52	61.50
"Narrow" . . . . .	46.2	67	72.50	36.15	89	123
<i>Rhomboidea</i> . . .	26.3	38	36.25	42.70	105	61.50

The figures are given separately to again call attention to the fact that open fertilization is no hindrance to pedigree work in *Capsella*. Since the seeds came from the same parent, we may add the results, which gives us *arachnoidea* 23.50 per cent., "narrow" 40 per cent. and *rhomboidea* 36.50 per cent. The fact that the percentage for "narrow" is too low and that for *rhomboidea* too high, while the percentage for *arachnoidea* is within the limits of probable error, is probably due to errors in classification, since greater weight was laid upon lobing of the adult leaves than upon comparative width of the earlier ones. The value of this culture lay chiefly in its suggestion of a zygotic combination *BBNn*, which prior to that time, on account of the gametic repulsion theory, was not supposed to exist. In consequence, a number of cultures were made, with the following result:

TABLE IV  
EVIDENCE OF HETEROZYGOTIC CHARACTER OF *Treleaseana* (*BBNn*)

Index No.	Number of Plants						Index No. of Parent	Char. of Parent	O or G	Char. of Grand-parent
	BBNN		BBNn		BBnn					
	Found	Ex-pected	Found	Ex-pected	Found	Ex-pected				
3,813	38	30	56	60	26	30	30,412AR2P6	BBNn	O	BBNn
3,913	36	44.75	87	89.50	56	44.75	30,412AR4P3	BBNn	O	BBNn
4,013	14	15.25	28	30.50	19	15.25	30,412AR6P3	BBNn	G	BBNn
4,213	15	28.50	65	57	34	28.50	30,412BR2P6	BBNn	O	BBNn
4,313	33	33	62	66	37	33	30,412BR6P5	BBNn	O	BBNn
4,413	37	45.25	102	90.50	42	45.25	30,412BR9P2	BBNn	O	BBNn
Total	173	196.75	400	393.50	214	196.75				

The "narrows" in question, then, fulfilled our expectation on the basis of a zygotic constitution *BBNn*. In some cases the percentages are too high, in others too low. The total yields fairly satisfactory results, to wit: *BBNN* 22 per cent., *BBNn* 51 per cent. and *Bbnn* 27 per cent. Two tests of the extracted recessive, a homozygotic *rhomboidea*, were made. The cultures, No. 3,713, from a guarded *rhomboidea* (30,412*AR2P3*) and No. 4,113, from an unguarded *rhomboidea* (30,412*AR8P3*), both derived from plants of the supposed zygotic constitution *BBNn*, yielded, respectively, 54 and 207 plants, all of which bore the typical *rhomboidea* characters.

In the cultures just tabulated, the plants of the supposed zygotic constitution *BBNn* resembled the parent in all respects. The form *arachnoidea*, in this case, must have the zygotic formula *BBNN*. Unfortunately, in this case also, it proved unfertile.

A better acquaintance with plants of the zygotic constitution *BBNn* led us to formulate certain differences between them and our original "narrow." Plants of the *BBNn* character, readily can be segregated from those of the *BbNn* character by somewhat narrower primary lobes, split to the midrib and the development, in climax leaves of well-grown specimens, of a secondary lobe, not pronounced but recognizable (Figs. 8, 9).

On the basis of these morphological differences, as well as because of the behavior of the plant on breeding, I propose to segregate it from type 4 under the name  $\times$  *Capsella Bursa-pastoris Treleaseana*. This form is homozygotic for *B*, while *Setchelliana* is heterozygotic for *B*. Both are heterozygotic for *N*. They may be expected to look alike during the early stages. Later they show a difference, since the form containing *Bb* does not develop sinuses as deep as the form containing *BB*. The form *Treleaseana*, when young, can readily be distinguished from a heterozygotic *rhomboidea* (*Bbnn*) by the relative width of the early leaves; later such a distinction is difficult (Figs. 4, 5, 7). If any distinction at all is to be made, it should be made on the basis of the rounding

of the lobes, those of *Treleaseana* being sharp, those of the heterozygotic *rhomboidea* rounded.

I am fully aware that in thus naming genotypes, I am departing from all rules laid down by systematists. But a rule is useful only as long as it serves a purpose. For the geneticist, the rules of systematists are of small value. Subspecies, variety, form, are, after all, but very general terms, almost incapable of definition because of too frequent abuse. But once we have determined the zygotic constitution of any plant, we have placed ourselves on a firmer basis. Behavior in breeding is the proper criterion. And while I recognize that this, for systematic purposes, is impracticable, at the same time I assert the right to use a trinomial for any organism of known zygotic constitution, this being, at the present time at least, the easiest way of designating any particular form. Some day we shall have formulas, corresponding to those of chemistry, to designate the lesser forms.

The increase in the number of named forms, a necessary consequence, need cause no alarm, since they concern only him who occupies himself with one species exclusively. But we must go even further than this. Squarely facing the issue, we find ourselves placed in a position which necessitates the naming of heterozygotes. Obviously, numerous objections could be urged. But since it has been shown, on the one hand, that certain forms can exist only in a heterozygous form (Baur's *Antirrhinum*) and, on the other, that not only the difference between the homozygote and the heterozygote is as great as that between many of our "systematic" species (for instance, *attenuata*, *bbNn*, and *arachnoidea*, *bbNN*), but that a homozygotic condition for a single gene gives the same result, whatever the condition of the other known genes, at least as thus far determined (*arachnoidea* occurs as *aaBBNN*, *aaBbNN* and *aabbNN*), the advantage of naming all forms of different zygotic constitution must be granted.

Thus far we have not encountered a plant of the zygotic constitution *BbNN*, at least as far as can be judged from

breeding experiments. On being selfed such a plant should yield:

$\frac{BN}{BN}$	$\frac{bN}{BN}$
$\frac{BN}{bN}$	$\frac{bN}{bN}$

It has been shown that plants of the zygotic constitution *BBNN* and *bbNN* exhibit the *arachnoidea* type. At least 50 per cent. of the offspring then should show this character. But if the suggestion made above is the correct one, *i. e.*, that all plants homozygotic for *N* exhibit the *arachnoidea* type, then the parent and its entire offspring should bear this character. The unfortunate infertility of *arachnoidea* prevents us from submitting this hypothesis to direct experimental proof. But there exist indirect means for establishing the probable truth of our contention. In the first place, we may cross two plants, the identity of which can be established beyond doubt, to wit, *attenuata* (*bbNn*) and *Treleaseana* (*BBNn*). Such a cross would yield:

$\frac{BN}{bN}$	$\frac{Bn}{bN}$
$\frac{BN}{bn}$	$\frac{Bn}{bn}$

Of these, we would recognize *Bbnn* because of its *rhomboida* character, 50 per cent. would be recognized as *Setchelliana* (*BbNn*), while the remainder, if our surmise is correct, would consist of *arachnoidea*. Experiments to determine this are under way. At the present we have another, though by far less accurate, means of testing our hypothesis. If the combination *NN* always results in a form *arachnoidea*, the offspring of a plant of the zygotic constitution *BbNn* would be composed of:

- 4 *Setchelliana* (*BbNn*),
- 2 *Treleaseana* (*BBNn*),
- 2 *attenuata* (*bbNn*),
- 4 *arachnoidea* (1 *BBNN*, 2 *BbNN*, 1 *bbNN*),

3 *rhomboidea* (1 *BbNn*, 2 *Bbnn*),  
1 *simplex* (*bbnn*).

Since *BbNn*, *BBNn* and *bbNn*, in the earlier experiments, might have been confounded in the later stages, and since there is little doubt as to the earlier stages, these three forms have been combined in Table V.

TABLE V  
RESULTS FROM SELECTED *Setchelliana* (*BbNn*)

Index No.	"Narrow"		<i>arachnoidea</i>		<i>rhomboidea</i>		<i>simplex</i>	
	Found	Expected	Found	Expected	Found	Expected	Found	Expected
26,912	134	157.6	94	78.8	68	59.1	19	19.7
3,613	94	89	45	45	33	33.75	8	11.25

This, especially in the case of No. 3,613, is a fairly close approximation to what we might expect. When in No. 3,613 we attempt to distinguish between *Setchelliana*, *Treleaseana* and *attenuata*, we get the following numbers, the expected numbers following in parentheses: *BbNn* 39(45), *BBNn* 21(22.50), *bbNn* 34(22.50), the last number being far too high. When the experiments were begun, we distinguished only between "narrow," "broad" and "linear." To-day we know that the "narrows" include *Treleaseana*, *Setchelliana* and *attenuata*, that the "broad" include *rhomboidea* and *simplex*, while the linears are identical with *arachnoidea*. In this light it is of interest to go back to the first generation of 1910. Our data yield the figures given in Table VI.

TABLE VI

Index No.	"Narrow"		"Linear"		"Broad"	
	Found	Expected	Found	Expected	Found	Expected
7,911	34	30.50	9	15.25	18	15.25
8,111	27	35.50	16	17.75	28	17.75
8,311	66	61	32	30.50	24	30.50
8,711	27	27	15	13.50	14	13.50
8,811	49	46.50	20	23.25	24	23.25
9,011	4	7.50	4	3.75	7	3.75
9,511	93	76	32	38	27	38
9,611	28	23.50	5	11.75	14	11.75
Total . . . . .	328	308.50	133	154.25	156	154.25
Per cent. . . . .	53.2	50	21.5	25	25.3	25

It must be granted that the approximation is fairly close, and that, taken in consideration with the others, it offers ample support for the correctness of the diagnosis of the zygotic constitution of the original plant. It at least offers a working basis. One would be tempted to accept it as a final solution were it not for the fortunate appearance of a plant which does not fit into our scheme and which, provisionally, has been named *Capsella Bursa-pastoris orbicularis*.

#### CAPSELLA BURSA-PASTORIS ORBICULARIS

This form differs from any other plant encountered in my cultures. While in a general manner resembling *simplex*, it differs in being more robust, having larger flowers (though not as large as those of *C. grandiflora*), and in having orbicular first leaves (Fig. 13). All leaves are covered with stout hairs. It is a plant which tempts us to draw a parallel between it and *Oenothera gigas*, a name which I have not used for the sake of avoiding an implied comparison.

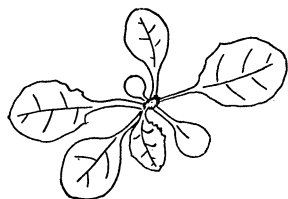


FIG. 13. SEEDLINGS OF *C. . . . orbicularis*.

The first plant of this type appeared in a culture of *attenuata* (26,012BR3P5) and was of sufficiently striking appearance, though but four or five leaves had developed, to call for a special note and a photograph. Later the plant was potted and finally seed was gathered from the unguarded plant. From this seed four seedlings were obtained. At least three of them closely resembled the parent, the fourth having somewhat narrower leaves. Later the differences between these plants and those of *simplex* became more apparent (Fig. 14). Those of my students to whom the differences have been pointed out have not the slightest difficulty in distinguishing between the two forms. It is hoped that later, when by means of prolonged cultures I shall have made myself more familiar with this form, it may be made the subject of a distinct paper where histological and cytological studies will find



a place. One would be inclined to look upon *orbicularis* as a mutation. But the fact that at first we classed *arachnoidea* as such, later to prove it of hybrid origin,<sup>17</sup>

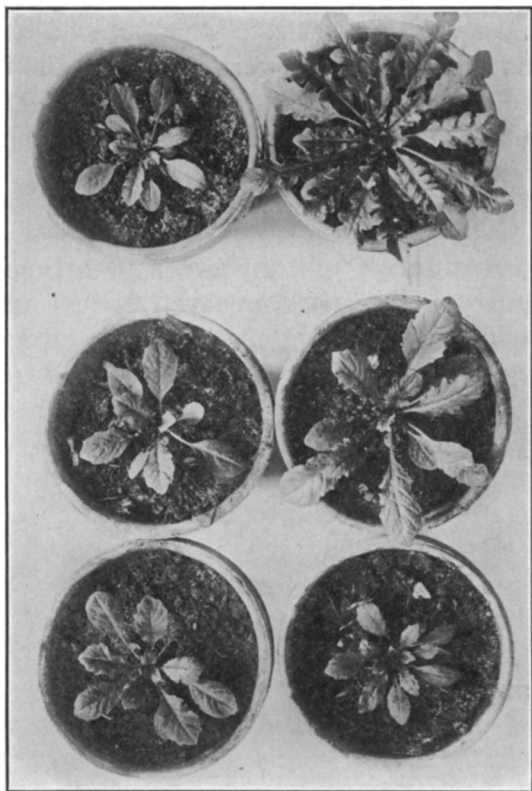


FIG. 14. FOUR SEEDLINGS OF *C. . . . orbicularis* AND (THE LOWER) TWO SEEDLINGS OF *C. . . . simplex*.

would tend to make us cautious, and lead us to attempt to find a solution for the origin of *orbicularis* in the dissociation or combination of certain "units." While I should not care to go quite as far as M. Heribert Nilson<sup>18</sup> "das ganze Mutations phänomen durfte unter einen gemeinsamen Gesichtspunkte: der Mendelschen Neukombination eingeordnet werden können," yet it is probable that here the majority of alleged mutations may be classed.

<sup>17</sup> Baur's (Vererbungslehre, 189) narrow-leaved *Melandrium album* is perhaps susceptible of the same explanation.

<sup>18</sup> *Zeitschr. f. ind. Abst. u. Bererb.*, 8: 89, 1912.

An examination of the herbarium material placed at my disposal reveals the fact that plants, apparently identical with *C. orbicularis*, occur in Europe. In the Engelmann herbarium of the Missouri Botanical Garden are two sheets (No. 3,661 and 3,664) containing specimens which undoubtedly must be classed here. The latter sheet bears the label: *Thlaspi Bursa-pastoris humile*. Heidelberg. April 1828.

A culture of *Capsella*, derived from seed of a single plant, unfortunately not preserved, escaped from cultivation in the Experiment Garden, and consisting of 182 individuals (Ehlers, No. 4,813), appears to be composed entirely of *orbicularis*. And while I have never encountered the plant in nature, these two facts lead us to another possible explanation. Perhaps the appearance of *orbicularis* in the original culture was due to an accidental admixture, such as is almost impossible to guard against when experimental plants are grown in a greenhouse used for a variety of purposes.

The exact relation which *orbicularis* bears to the other types of *Capsella* here described can, of course, be determined only after a series of experiments has been carried out. However, the delay in the completion of the manuscript, caused by the unfortunate destruction, by fire, of the botanical laboratories of the University of Michigan, enables me to add that a third generation of *orbicularis*, the parent being No. 32,012R1P3, shows at least two and possibly three types, of which one is especially interesting in having rather narrow leaves, at least as compared with those of typical *orbicularis*. The contrast between the two forms is increased by the fact that in the narrow-leaved form the foliage is entirely glabrous, while in the typical *orbicularis* the leaves are covered with numerous stiff, almost bristle-like, hairs.

#### X *CAPSELLA BURSA-PASTORIS ARACHNOIDEA*

By this name is designated the linear-leaved form, the appearance of which induced us to undertake the cultivation of *Capsella Bursa-pastoris Setchelliana*.

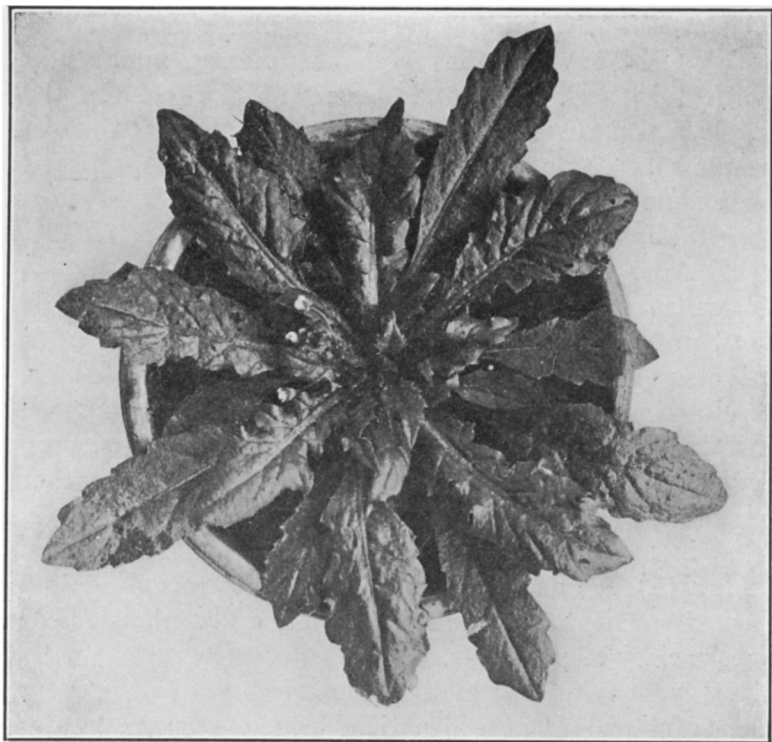
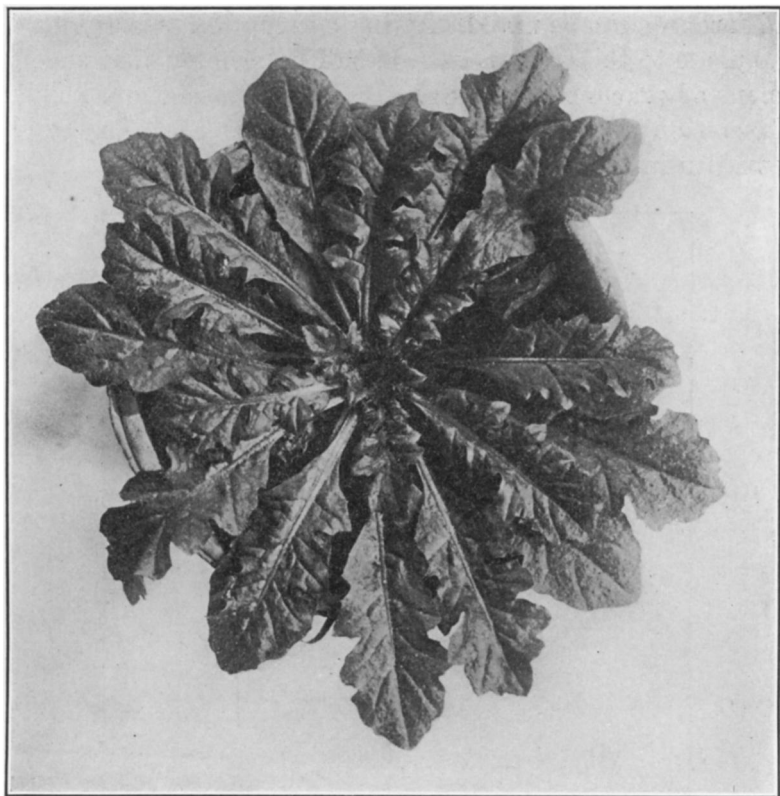


FIG. 15. ROSETS ILLUSTRATING THE TWO TYPES

Already the leaves which immediately follow the cotyledons serve to distinguish plants of this type from all others. At the ten-leaf stage even the casual observer is able to segregate them at once from the other rosets. The leaves are acicular and the cotyledons far larger than those of the seedlings of the other forms. The greater size of the cotyledons may be attributed to the insufficiency of the subsequent leaves.

If one removes the terminal bud of seedlings of *Atriplex hortensis* or one of its color varieties, it will be found that the cotyledons increase in length far beyond normal, sometimes reaching a length of 8 cm. Under favorable conditions the leaves of  $\times C. arachnoidea$  may reach a length of 100 mm., with a greatest width of 6 mm. (Fig. 16). The stem ordinarily is weak, having a diameter of only 1 mm. It may reach a length of 30 cm. (Fig. 17).



THUS FAR RECOGNIZED IN *C. . . . orbicularis*.

The flowers are small, the petals especially so. The anthers shrivel up early and as a rule are devoid of pollen grains. Occasionally a few can be demonstrated. The ovary, though small, contains what appear to be ovules capable of being fertilized. Thus far I have collected eight seeds contained in 6 capsules on unguarded plants of *arachnoidea* (Fig. 18). Two of these germinated, the one yielding a plant which looks like *simplex*, though having a large amount of red coloring matter in the petioles, while the other is an *arachnoidea*. Attempts to artificially fertilize *arachnoidea* have failed absolutely.

As has been shown above, one may distinguish, on the basis of genotypic constitution, three forms of *arachnoidea*, viz.: *BBNN*, *BbNN* and *bbNN*. Externally no

differences can be noted. A single exception perhaps may be made to this statement. It had been noted that specimens of *arachnoidea* frequently showed fasciation. This fasciation seems most marked in plants of the zygotic constitution *BBNN* (Figs. 19, 20, 21).

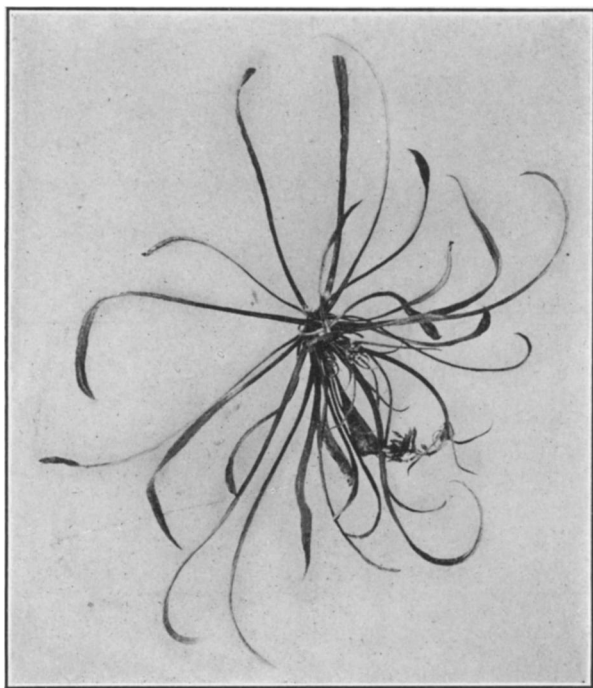


FIG. 16. ROSET OF  $\alpha$  *C. . . . arachnoidea*.

While it is hoped that later a more extended report may be made upon this plant, at present it may be stated that there exists the probability that it may throw some light upon the nature of fasciations. In earlier publications<sup>19</sup> I have brought together some of the known facts bearing upon this teratological character. Though a large por-

<sup>19</sup> "Fasciation in *Oxalis crenata* and Experimental Production of Fasciations," *Rep. Mo. Bot. Gard.*, 17: 147, 1906; "Fasciations of Known Causation," *AMERICAN NATURALIST*, 42: 81, 1908; "Inheritance of Fasciation in *Zea Mays*," *The Plant World*, 14: 1911; "The Origin of Species in Nature," *AMERICAN NATURALIST*, 45: 641, 1911; "Frondescence and Fasciation," *Plant World*, 14: 1911; "Fasciation in *Oxalis crenata*," *Botanical Journal*, 2: 111, 1913.

tion of the experimental garden is devoted to cultures of fasciated races, nothing further has been determined than that the fasciated character is inherited, that it is transmitted through non-fasciated individuals, that its apparentness depends upon nutrition, that it behaves as a



FIG. 17. TWO HERBARIUM SPECIMENS OF  $\times$  *C. . . . arachnoidea*.

recessive character and that the fasciated character of the stem appears to be associated with split leaves and cup-shaped leaves. In a paper read before the Research Club of the University of Michigan on March 16, 1910, and announced under the title "The Identity and Inheritance of Teratological Characters," I showed that split leaves, ascidia, certain disturbances in the arrangement of the

flowers, supernumerary locules in the fruit, etc., may safely be taken as an indication of the presence of the fasciated character. More recently, Kajanus,<sup>20</sup> working

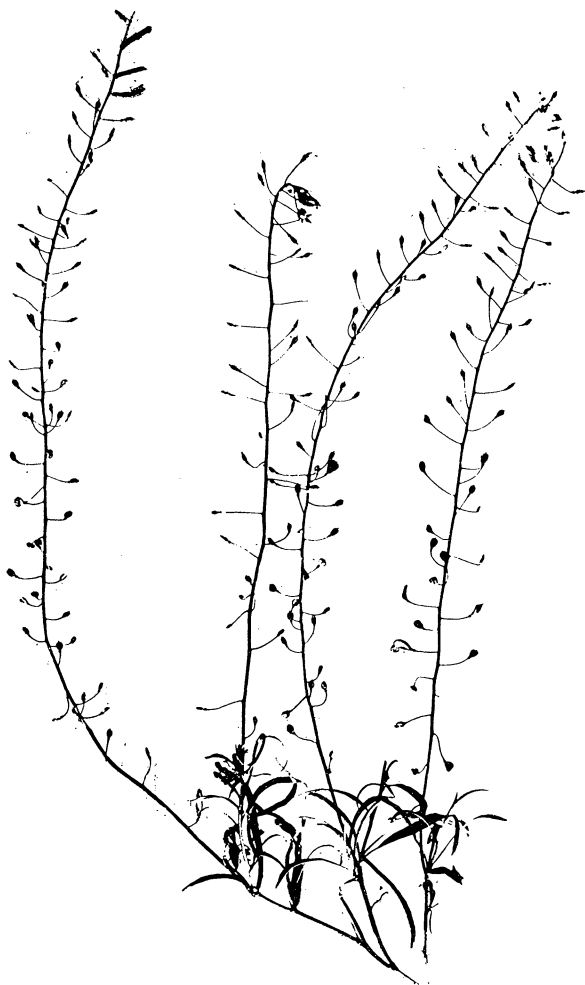


FIG. 18. SHOOT OF *C. . . . arachnoidea*, WITH A LARGE NUMBER OF INFERTILE AND FEW FERTILE CAPSULES.

with different material, has fully confirmed the views which I expressed at the time. This is of particular in-

<sup>20</sup> Kajanus, B., "Polyphyllie und Fasziation bei *Trifolium pratense* L.," *Zeitsch. f. ind. Abst. u. Vererb.*, 7: 63, 1912; "Ueber einige vegetative Anomalien bei *Trifolium pratense* L., *ibid.*, 9: 111, 1913.

terest in connection with *Capsella arachnoidea*, since many of the plants which do not show a fasciated stem do show split leaves (Fig. 20) and a most peculiar whorling of the flowers (Fig. 21).



FIG. 19. FASCIATED PLANT OF *x C. . . . arachnoidea*.

The spatulate condition of the leaves of the seedling shown in Fig. 2 is believed to have been due to fasciation.

*Capsella Bursa-pastoris arachnoidea*, then, bears all the earmarks of a fasciated race. All of the three zygotic combinations which yield the *arachnoidea* type are homozygotic for *N*. The recent work of East and Hayes, and of Emerson on *Zea Mays* has shown that the fasciated



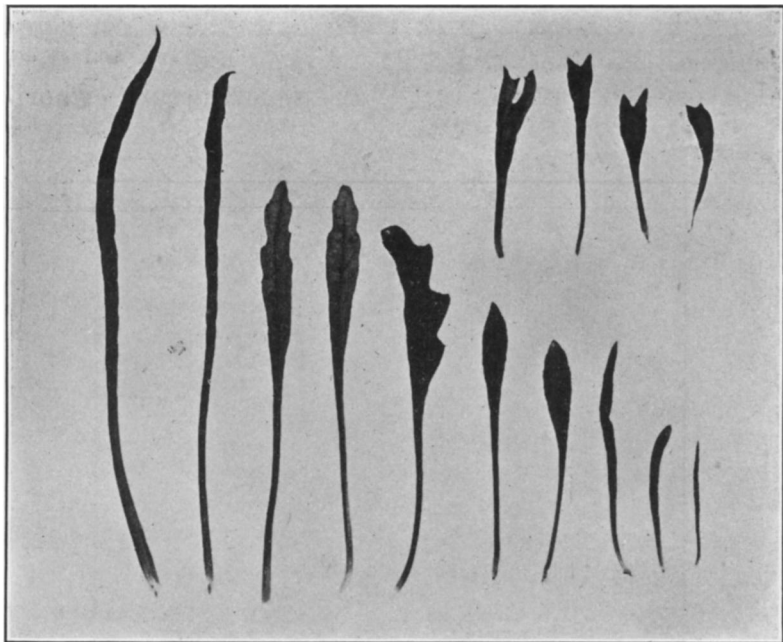


FIG. 20. LEAVES OF *x C. . . . arachnoidea*.

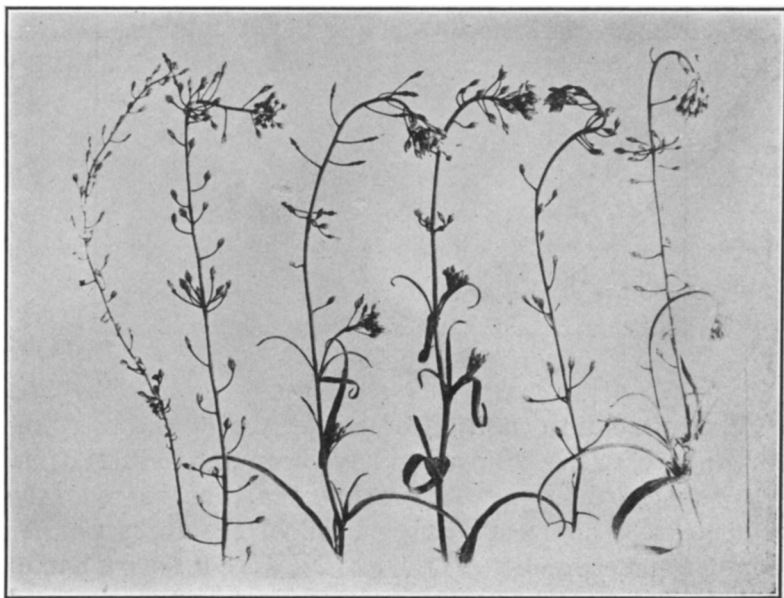


FIG. 21. ABNORMAL WHORLED ARRANGEMENT OF THE FLOWERS IN INFLORESCENCES OF *x C. . . . arachnoidea*.

character is dominant, though Mendel, in his experiments with *Pisum umbellatum*, has shown it to be recessive. No fasciation, thus far at least, has been noted in the other forms used in these experiments.

#### SUMMARY

A culture of *Capsella Bursa-pastoris* proved heterozygotic, yielding certain new forms ( $\times$  *C. Bursa-pastoris Setchelliana*,  $\times$  *C. Bursa-pastoris Treleaseana*,  $\times$  *C. Bursa-pastoris arachnoidea* and  $\times$  *C. Bursa-pastoris attenuata*), as well as certain forms already described by Shull (*C. Bursa-pastoris rhomboidea* and *C. Bursa-pastoris simplex*) in the proportion 4:2:4:2:3:1. The distinction between *simplex* and *rhomboidea*, both *inter se* and between them and the other forms, is readily made by any one familiar with Shull's investigations. These two plants agree in having the earlier leaves broad (Fig. 4). The climax leaves of *rhomboidea* and *simplex* show marked differences, especially as far as the incision of the blade is concerned. These incisions, in *simplex*, reach a depth equal to approximately one fourth of the width of the blade (Fig. 10). In *rhomboidea* the incisions are deeper, reaching the midrib in the homozygous form (Fig. 12). The leaves of the latter also show marked secondary lobes.

The distinction between  $\times$  *C. Bursa-pastoris Setchelliana*,  $\times$  *C. Bursa-pastoris Treleaseana* and  $\times$  *C. Bursa-pastoris attenuata* is made with greater difficulty. They agree in having long and narrow first leaves. The climax leaves of *Treleaseana* and *Setchelliana* show marked incisions, exceeding one fourth of the width of the blade, and which may reach the midrib (Fig. 9). The latter form also may show marked secondary lobes.

Besides the phenotypes here mentioned occur two others, the one,  $\times$  *C. Bursa-pastoris orbicularis*, with an almost orbicular first leaf (Fig. 13) and a climax leaf greatly resembling that of *simplex* (Figs. 14, 15), though differing in texture. This form has not been sufficiently studied, but is believed to be identical with one known to

occur in Europe. Finally there is  $\times C. Bursa-pastoris arachnoidea$ , a sterile, linear-leaved form, with a weak stem and which frequently shows fasciation (Figs. 17–21). To facilitate a distinction between these forms, a key is appended:

- |  |                      |
|--|----------------------|
| a. Early leaves broad.                                     |                      |
| b. Early leaves orbicular.                                 | <i>orbicularis.</i>  |
| bb. Early leaves twice as long as broad.                   |                      |
| c. Climax leaves incised to midrib.                        | <i>rhomboidea.</i>   |
| cc. Early leaves not incised to midrib.                    | <i>simplex.</i>      |
| aa. Early leaves long and narrow.                          |                      |
| b. Early leaves acicular.                                  | <i>arachnoidea.</i>  |
| bb. Early leaves $2\frac{1}{2}$ –3 times as long as broad. |                      |
| c. Climax leaves not incised to midrib.                    | <i>attenuata.</i>    |
| cc. Climax leaves incised to or almost to the midrib.      |                      |
| d. Secondary lobes pronounced.                             | <i>Treleaseana.</i>  |
| dd. Secondary lobes absent.                                | <i>Setchelliana.</i> |

It was found that, besides the genes *A*, *B*, *C* and *D*, whose existence was shown by Shull, there exists another gene, *N*, responsible for the narrow character of the earlier leaves. For the various forms, mentioned here, the following zygotic constitutions have been tentatively determined: *simplex*, *bbnn*; *rhomboidea*, *BBnn* and *Bbnn*; *Setchelliana*, *BbNn*; *Treleaseana*, *BBNn*; *attenuata*, *bbNn*; *arachnoidea*, *BBNN*, *BbNN* and *bbNN*. The zygotic constitution of *orbicularis* has not been determined.

As to the probable origin of  $\times C. Bursa-pastoris$  *Setchelliana*, little can be said. It most probably results from a cross between *rhomboidea* and *attenuata* (*BBnn*  $\times$  *bbNn*). This seems the most plausible explanation since, judging from herbarium specimens, both *attenuata* and *rhomboidea* occur throughout the United States. Unfortunately such an assumption necessitates an explanation of the origin of *attenuata*.

My thanks are due to the regents of the University of Michigan for the facilities placed at my disposal, to head-gardener Adolph Weiner for his constant care of the experimental plants, to Messrs. J. H. Ehlers, A. Povah, C. Oberlin and A. W. Murdock for assistance in classification of the seedlings and to the director of the Missouri Botanical Garden for the loan of herbarium material.

## CONCLUSIONS

1. Besides the genes (*A*, *B*, *C*, *D*) discovered by Shull, there exists in *Capsella* a gene *N*, responsible for the narrow character of the early leaves of certain forms.

2. Absence of the gene *N* results in the formation of early leaves of a "broad" character.

3. The form designated *arachnoidea* is of hybrid origin, as are the forms *Setchelliana*, *Treleaseana* and *attenuata*.

4.  $\times$  *Capsella Bursa-pastoris arachnoidea* is formed whenever the plant is homozygotic for *N*, whatever the constitution of the remainder of the zygote (*BBNN*, *BbNN*, *bbNN*), i. e., a homozygous condition for the presence of a single factor may overshadow the influence of others.

5. Homozygosity for a single factor may be responsible for total, or almost total, sterility.

6. A knowledge of the early stages, as well as of the climax leaves, is essential for the classification of the phenotypes of *Capsella Bursa-pastoris*.